RED-COCKADED WOODPECKER NUTRITIONAL STATUS IN RELATION TO HABITAT: EVIDENCE FROM PTILOCHRONOLOGY AND BODY MASS

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Abstract: Sexual divergence in foraging behavior exhibited by red-cockaded woodpeckers (*Picoides borealis*) should reduce intersexual competition for foraging sites. Males tend to forage at greater heights and on smaller stem diameters than females. It is well known that red-cockaded woodpeckers have an aversion to a well-developed stratum of midstory vegetation. Foraging areas with increased midstory vegetation may cause females to increase their foraging height, thus bringing them into greater competition with males. It has been suggested that female red-cockaded woodpeckers, to a greater extent than males, may suffer nutritional stress due to a reduction in foraging niche under certain conditions. In eastern Texas, we measured growth bars of red-cockaded woodpecker rectrices using the techniques of ptilochronology to obtain an index of nutritional status of individual woodpeckers during the period of feather growth. Total rectrix length and body mass were also obtained as additional measures of nutritional status. Data were acquired from 2 forest types determined by the dominant pine species in the overstory: (1) longleaf pine (*Pinus palustris*) habitat which is relatively devoid of well-developed midstory vegetation, and (2) mixed loblolly pine (*P. taeda*)-shortleaf pine (*P. echinata*) habitat where midstory vegetation was generally well-developed. We compared width of 6 growth bars, rectrix length, and body mass between birds occupying these 2 pine habitats using 2-factor analyses of variance with pine habitat and molt year as the main effects. These were followed by a least significant-difference test. Adult males and adult females were tested separately. Width of 6 growth bars and rectrix length were similar for adult males in longleaf pine and loblolly-shortleaf pine habitats, but body mass was greater in the latter. Width of 6 growth bars, rectrix length, and body mass were all greater for adult females in loblolly-shortleaf pine habitat than in longleaf pine habitat. Our results indicate that red-cockaded woodpeckers are generally more nutritionally fit in loblolly-shortleaf pine than in longleaf pine habitat in eastern Texas despite more adverse midstory conditions in the former. They also suggest adult females may experience greater nutritional stress than adult males.

Key words: habitat, nutrition, *Picoides borealis*, ptilochronology, red-cockaded woodpecker, Texas.

Red-cockaded woodpeckers inhabit fire-climax pine forests of the southeastern United States (Jackson 1971). The species is a cooperative breeder, living in social units typically consisting of the breeding pair, 0-3 male helpers, and offspring of the year (Ligon 1970, Lennartz et al. 1987, Walters et al. 1988*a*).

Red-cockaded woodpeckers forage predominately in live pines (*Pinus* spp.) with minor use of recently dead pines and other genera (Ligon 1970, Hooper and Lennartz 1981, Delotelle et al. 1983). Each social unit typically forages as a group (Hooper and Lennartz 1981) and uses a foraging area of 14.2 to over 400 ha (Crosby 1971*b*, Sherrill and Case 1980, Patterson and Robertson 1981, Hooper et al. 1982, Nesbitt et al. 1983, Jackson and Schardien-Jackson 1986).

Red-cockaded woodpeckers exhibit sexual divergence in foraging behavior with males foraging at greater heights and on smaller average stem diameters than females (Ligon 1968; Ramey 1980; Hooper and Lennartz 1981; C. Rudolph et al., U.S. Forest Service, unpublished data). Sexual divergence in foraging niches can result from genetic differences or behavioral interactions. In the genus *Picoides*, both genetic (Jackson 1970*b*, Williams 1980) and behavioral (Ligon 1968; Hogstad 1976, 1978) mechanisms have been hypothe-

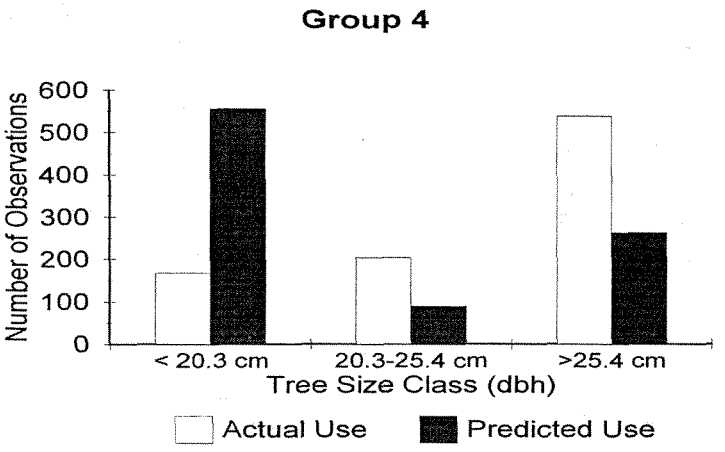

Figure 12. Foraging of red-cockaded woodpeckers in Group 4 versus availability of pine trees by tree size class within 800 m of group nest tree at the Savannah River Site, South Carolina (1992 to 1995).

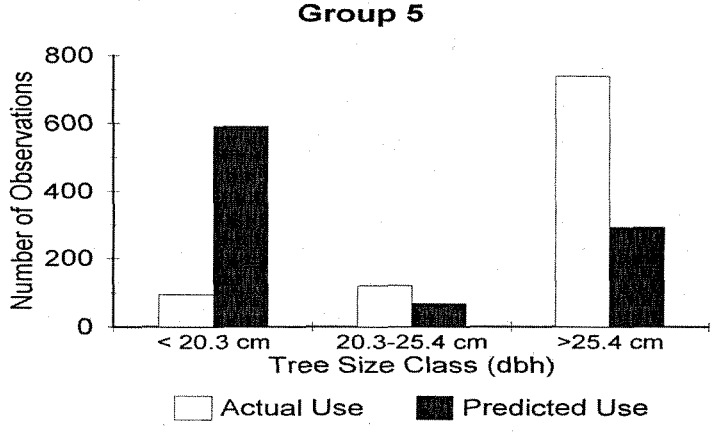

Figure 13. Foraging of red-cockaded woodpeckers in Group 5 versus availability of pine trees by tree size class within 800 m of group nest tree at the Savannah River Site, South Carolina (1992 to 1995).

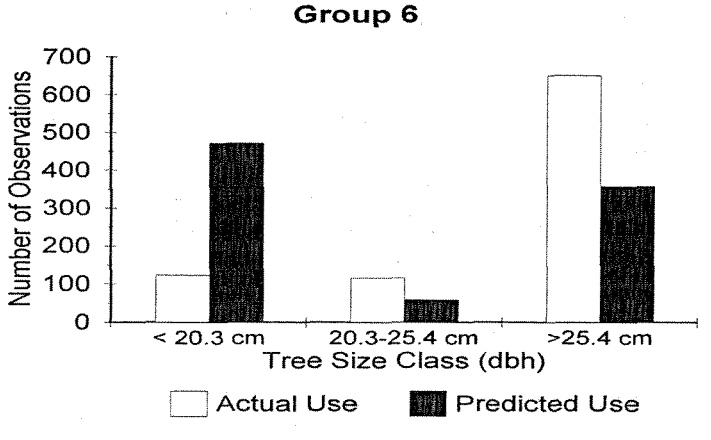

Figure 14. Foraging of red-cockaded woodpeckers in Group 6 versus availability of pine trees by tree size class within 800 m of group nest tree at the Savannah River Site, South Carolina (1992 to 1995).

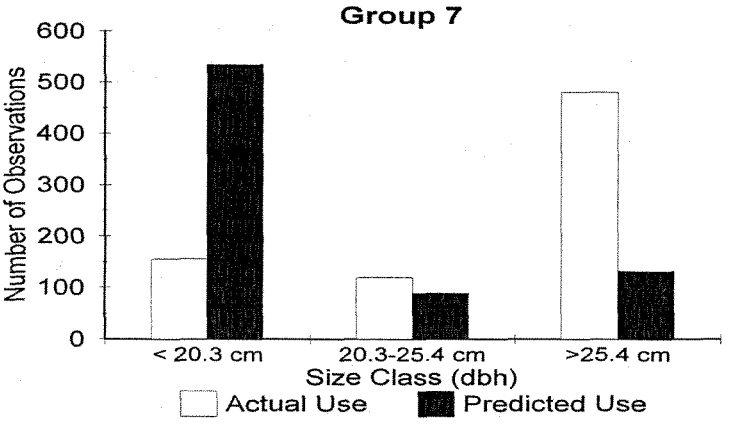

Figure 15. Foraging of red-cockaded woodpeckers in Group 7 versus availability of pine trees by tree size class within 800 m of group nest tree at the Savannah River Site, South Carolina (1992 to 1995).

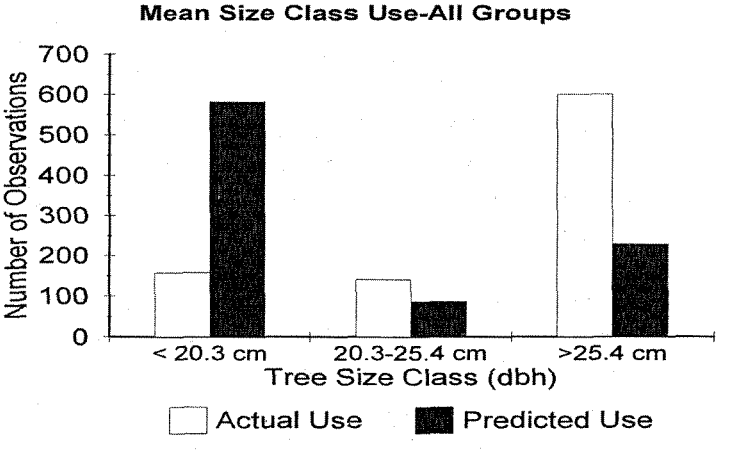

Figure 16. Mean tree use by foraging of red-cockaded woodpeckers, all groups combined, versus mean availability of pine trees by tree size class within 800 m of group nest trees at the Savannah River Site, South Carolina (1992 to 1995).

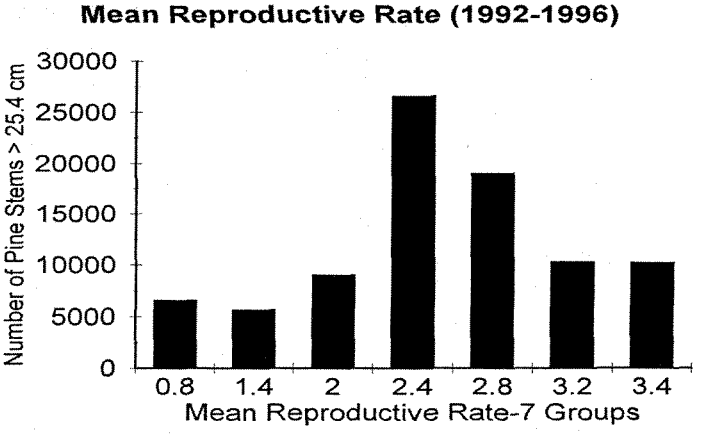

Figure 17. Red-cockaded woodpeckers mean reproductive rate versus number of pine stems greater than 25.4 cm dbh and within 800 m of the nest tree.

sized. Evidence supporting the behavioral hypothesis has been provided in the case of the downy woodpecker (*P. pubescens*) by Kilham (1970) and Peters and Grubb (1983).

It has been suggested that female red-cockaded woodpeckers, to a greater extent than males, may suffer nutritional stress due to a reduction in foraging niche under certain conditions (J. Jackson, Florida Gulf Coast University, personal communication). Red-cockaded woodpeckers select larger pines for foraging (Hooper and Lennartz 1981, Delotelle et al. 1983, Engstrom and Sanders 1997, Zwicker and Walters 1999). On smaller trees the spatial separation between females and males is reduced (Ramey 1980, Jackson and Schardien-Jackson 1986). If males are behaviorally dominant, the detrimental effects of foraging on smaller pines may be more severe for females.

Midstory vegetation, especially broadleaf species, surrounding cavity trees has been shown to have a negative effect on red-cockaded woodpeckers (Grimes 1977, VanBalen and Doerr 1978, Locke et al. 1983, Conner and Rudolph 1989, Loeb et al. 1992). More recently, the negative effects of midstory vegetation within foraging habitat have been investigated (Epting et al. 1995, Davenport et al. 2000, Walters et al. 2002*b*). Results from Rudolph et al. (2002) indicate that red-cockaded woodpeckers tend to avoid dense midstory vegetation by increasing foraging height. Consequently, the female foraging niche may be compressed by midstory vegetation from below, and by the behaviorally dominant male from above.

We measured growth bar width and total feather length of red-cockaded woodpecker rectrices using the techniques of ptilochronology to obtain an index of the nutritional status of individual woodpeckers during the period of feather growth. We also obtained the body mass of each individual. We used the resulting data to examine the nutritional status of red-cockaded woodpeckers in relation to habitat.

Ptilochronology is the study of feather growth rates by examining growth bars visible under proper light conditions. Growth bars are alternating light and dark bands oriented approximately perpendicular to the rachis (Riddle 1908). An adjacent light and dark pair consists of feather material incorporated during a 24-hr period of growth (Michener and Michener 1938, Wood 1950). Nutritional status, especially available energy, influences the rate of feather growth (Grubb 1989, 1991; Jenkins et al. 2001), but see comments on the limits of the methodology (Murphy and King 1991, Grubb 1992, Murphy 1992). Ptilochronology has been used successfully to examine hypotheses relating to the effects of supplemental food (Grubb 1989, Waite 1990), brood size (White et al. 1991), and habitat quality (Carlson 1998, Grubb et al. 1998) in a variety of bird species.

STUDY AREA AND METHODS

We examined the nutritional status of red-cockaded woodpeckers in 2 forest types (longleaf pine versus loblolly-shortleaf pine) using width of 6 growth bars, rectrix length, and body mass as measures of nutritional status. Feathers and body mass were obtained from red-cockaded woodpeckers on the Angelina National Forest (ANF; 31° 15'N, 94° 15'W) and Davy Crockett National Forest (DCNF; 31° 21'N, 95° 07'W) in eastern Texas. Longleaf pine is prevalent on much of the southern ANF. Loblolly pine, shortleaf pine, or a mixture of the 2, dominate the northern ANF and DCNF. The outermost pair of the 12 rectrices in woodpeckers is rudimentary (Short 1982). Consequently, the fifth rectrix from the center on the right side (R-5) was collected for analysis. All rectrices were assumed to have been formed during the normal period of the annual molt. This period for rectrices in red-cockaded woodpeckers is from August to November (Jackson 1983). Feathers were collected from June 1989 to November 1990.

Social status (i.e., breeder, helper, juvenile), sex, and body mass were recorded for each woodpecker. Each bird was also fitted with a unique color combination of leg bands for individual recognition. The adult male roosting in the most recently used nest cavity was assumed to be the breeding male (Ligon 1970). All other adult males were assumed to be helpers. The adult female, almost always 1 per group in our sample, was assumed to be the breeding female. Behavioral observations, particularly during the nesting season, were used to support these assignments of social status. Juveniles were identified and sex was determined by their distinctive juvenile plumages (Jackson 1983).

Each woodpecker was assigned to 1 of 2 forest types determined by the dominant pine species in the overstory. Longleaf pine habitats were heavily dominated by this pine species, and due to the greater frequency and impact of fire in this habitat, were relatively devoid of well-developed midstory vegetation. Loblolly and shortleaf pine habitats were dominated by 1 or a mixture of these 2 pine species and were

combined in the analyses. Due to site differences and the reduced impact of fire in these habitats, midstory vegetation was generally well-developed.

Measurement of growth bars was done using the methods of Grubb (1989). A dial caliper was used for all measurements which were made to the nearest 0.01 mm. Total rectrix length was measured, and the point two-thirds of the total length from the proximal end determined. The total width of 6 growth bars measured consisted of the bar at the two-thirds point plus 2 distal and 3 proximal bars adjacent to it.

Birds were captured either in the morning just prior to emergence from their roosting cavity, or in the evening just after they roosted, and then weighed. Each woodpecker was weighed to the nearest 0.5 g using a 100 g Pesola scale. We realize there is temporal variability in the weight of a given individual over a 24-hour period. However, morning and evening weights were pooled for each of the 2 pine forest types, and pine habitats were compared statistically.

Only adult birds were used in analyses of longleaf pine versus loblolly-shortleaf pine habitats. Breeders and helpers were combined into adult males and adult females, and the sexes were analyzed separately. We compared nutrition variables (6 growth bars, rectrix length, and body mass) between pine habitats (longleaf pine and loblolly-shortleaf pine) and among molt years (1988, 1989, and 1990) using 2-factor analyses of variance. Rectrix length and body mass for males and females were rank-transformed prior to analyses of variance due to lack of normality or heterogeneous variances. Each analysis of variance was followed by a least significant-difference test for the detection of differences between molt years. The criterion for significance in all statistical tests was $P < 0.05$.

RESULTS

The width of 6 growth bars and rectrix length of adult male red-cockaded woodpeckers were similar between longleaf pine and loblolly-shortleaf pine habitats, but body mass was significantly greater in the latter (Table 1). We detected no differences between molt years in width of 6 growth bars, rectrix length, or body mass for adult males (Table 2). There were no significant interactions between pine habitat and molt year.

The width of 6 growth bars, rectrix length, and body mass of adult female red-cockaded woodpeckers were all significantly greater in loblolly-shortleaf pine habitat than in longleaf pine habitat (Table 1). All 3 measures of nutrition were significantly less for adult females in 1988 than in 1989 or 1990 (Table 2). There was no significant interaction between pine habitat and molt year relative to width of 6 growth bars, rectrix length, or body mass.

DISCUSSION

Adult male red-cockaded woodpeckers had similar growth bar widths and rectrix lengths in longleaf pine and loblolly-shortleaf pine habitats. However, body mass was significantly greater in loblolly-shortleaf pine habitat, indicating that males in longleaf pine habitat may be nutritionally less fit. Adult females in longleaf pine habitat had narrower growth bars, shorter rectrices, and weighed less suggesting a lower nutritional fitness than for adult females in loblolly-shortleaf pine habitat.

Table 1. Means (± SD) for width of 6 growth bars, rectrix length, and body mass for adult male and adult female red-cockaded woodpeckers in longleaf pine and loblolly-shortleaf pine habitats in eastern Texas.

Adult Males				
Nutrition Variable	Longleaf	Loblolly-shortleaf	F^a	P^a
Width of 6 Growth Bars (mm)	15.3 ± 0.8, n = 22	15.3 ± 1.3, n = 25	0.15	0.702
Rectrix Length (mm)[b]	60.6 ± 2.1, n = 22	61.6 ± 2.6, n = 25	3.11	0.085
Body Mass (g)[b]	47.6 ± 2.7, n = 22	49.0 ± 2.1, n = 25	4.95	0.032
Adult Females				
Nutrition Variable	Longleaf	Loblolly-shortleaf	F^a	P^a
Width of 6 Growth Bars (mm)	14.9 ± 1.4, n = 15	15.7 ± 1.2, n = 15	7.76	0.010
Rectrix Length (mm)[b]	60.7 ± 4.1, n = 15	62.7 ± 3.7, n = 16	9.30	0.005
Body Mass (g)[b]	45.4 ± 2.1, n = 16	46.8 ± 2.3, n = 16	6.47	0.017

[a]2-factor analysis of variance.
[b]Rectrix length and body mass for males and females were rank-transformed prior to analyses of variance due to lack of normality or heterogeneous variances.

Adult males in each pine habitat, especially the socially dominant breeding males, presumably frequent the more desirable foraging locations within a tree. Thus, any differences between the 2 pine habitats that may affect female nutrition may not affect the males as severely. This may explain why only body mass was different between pine habitats for males whereas all 3 nutritional indices were different for females, thereby lending support to J. Jackson's (personal communication) hypothesis that female red-cockaded woodpeckers may suffer greater nutritional stress than males due to a reduction in foraging niche under certain conditions. Body mass data were collected in each pine habitat throughout the year. Thus, body mass reflects the average nutritional condition of woodpeckers throughout the year, whereas growth bar width and feather length reflect the average nutritional condition only during the period of molt of rectrices (i.e., August-November).

Midstory vegetation was generally well-developed in loblolly-shortleaf pine habitat, and longleaf pine habitat was relatively devoid of midstory vegetation. It is known that male red-cockaded woodpeckers forage at greater heights than females (Ligon 1968; Ramey 1980; Hooper and Lennartz 1981; C. Rudolph et al., U.S. Forest Service, unpublished data). It is also known that midstory vegetation, especially broadleaf species, has a negative effect on red-cockaded woodpeckers (Grimes 1977, VanBalen and Doerr 1978, Locke et al. 1983, Conner and Rudolph 1989, Loeb et al. 1992). Rudolph et al. (2002) obtained midstory height and midstory density data at randomly selected canopy trees within both pine habitats simultaneous to this study and within the same forests from which our woodpecker data were obtained. They measured midstory density using a five-measure scale ranging from none (1) to very dense (5). They reported both midstory height (longleaf = 8.3 m, loblolly-shortleaf = 10.7 m; $P = 0.02$) and midstory density (longleaf = 2.4, loblolly-shortleaf = 3.6; $P < 0.0001$) to be significantly greater in loblolly-shortleaf pine habitat. Rudolph et al. (2002) also found that red-cockaded woodpeckers tend to avoid taller and denser midstory by increasing their foraging height. Therefore, it seems that females in loblolly-shortleaf pine habitat, where midstory conditions are worse, would be forced to forage higher than usual and risk confrontation with males (especially the breeding male). Females of the more open longleaf pine habitat would presumably not be as affected in this way.

The canopy height of loblolly and shortleaf pines was considerably greater than that of longleaf pines in our study area (Schaefer 1996, Rudolph et al. 2002). Greater canopy height may help offset some of the negative effects of midstory vegetation on female foraging height in loblolly-shortleaf pine habitat since a greater proportion of a given pine would extend above the midstory level. Rudolph et al. (2002) indicate that red-cockaded woodpeckers concentrate foraging activities in or adjacent to areas with reduced midstory vegetation. If red-cockaded woodpecker groups in loblolly-shortleaf pine forest often seek foraging areas relatively devoid of midstory vegetation (i.e., seed tree/shelterwood stands and the area immediately surrounding cavity trees where midstory removal has

Table 2. Means (± SD) for width of 6 growth bars, rectrix length, and body mass of adult male and adult female red-cockaded woodpeckers during the 1988, 1989, and 1990 molt years in eastern Texas.

Adult Males			
	Molt Year [a]		
Nutrition Variable	1988	1989	1990
Width of 6 Growth Bars (mm)[b]	15.1 ± 1.1^{A} $n = 18$	15.6 ± 1.2^{A} $n = 12$	15.3 ± 0.9^{A} $n = 17$
Rectrix Length (mm)[b]	60.6 ± 2.7^{A} $n = 18$	60.9 ± 1.7^{A} $n = 12$	61.8 ± 2.5^{A} $n = 17$
Body Mass (g)[b]	47.6 ± 3.0^{A} $n = 18$	49.1 ± 2.4^{A} $n = 12$	48.6 ± 1.7^{A} $n = 17$

Adult Females			
	Molt Year [a]		
Nutrition Variable	1988	1989	1990
Width of 6 Growth Bars (mm)[b]	14.2 ± 1.3^{A} $n = 10$	16.0 ± 0.9^{B} $n = 11$	15.6 ± 1.1^{B} $n = 9$
Rectrix Length (mm)[b]	58.8 ± 5.1^{A} $n = 11$	63.6 ± 1.7^{B} $n = 11$	63.0 ± 2.2^{B} $n = 9$
Body Mass (g)[b]	45.1 ± 2.6^{A} $n = 11$	47.1 ± 2.3^{B} $n = 11$	46.0 ± 1.6^{AB} $n = 10$

[a]Longleaf pine and loblolly-shortleaf pine habitats are combined.
[b]Different letters indicate significant differences (alpha = 0.05) between years for each nutrition variable as indicated by least significant-difference tests following 2-factor analyses of variance.

taken place), then it seems females would not be forced to forage higher as often. This should reduce foraging competition and possible conflict with males.

Greater growth bar width, rectrix length, and body mass for adult females, and greater body mass for adult males indicate that adult red-cockaded woodpeckers are nutritionally more fit in loblolly-shortleaf pine habitat than in longleaf pine habitat despite the generally much worse midstory conditions in the former. Schaefer (1996) observed nestling provisioning by adult red-cockaded woodpeckers in eastern Texas using the same woodpecker groups and within the same time period our data were obtained. Prey availability was significantly greater, in terms of prey biomass delivered to nestlings, in loblolly-shortleaf pine habitat despite taller and denser midstory within that habitat type. Collins et al. (2002) showed prey availability to be greater in pine habitats with less midstory vegetation and more herbaceous vegetation. The seemingly contradictory results among these studies regarding relationships between prey availability and midstory vegetation are likely due to differences in pine species rather than midstory conditions. Schaefer (1996) also noted a significantly higher degree of southern pine beetle (*Dendroctonus frontalis*) activity in loblolly-shortleaf pine habitat (i.e., number of beetle spots, number of infested pines, and number of infested hectares) during that time period. It is well known that both loblolly and shorteaf pines are much more likely to succumb to southern pine beetle attack than longleaf pine (Hodges et al. 1979). Red-cockaded woodpeckers often concentrate foraging activities on dying pines infested with various arthropods (C. Rudolph, U.S. Forest Service, unpublished data). The greater number of dying trees among loblolly and shortleaf pines in our study area probably resulted in an increase in prey availability within this forest type. This increase may have been substantial enough to more than offset any negative effects of more abundant midstory in loblolly-shortleaf pine habitat, resulting in an overall better nutritional condition for red-cockaded woodpeckers in that forest type.

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